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Published in:
Journal of Vegetation Science

Publication date:
1999

Journal of Vegetation Science 10: 111-122, 1999

Nutrient limitation and vegetation changes in a coastal dune slack

Lammerts, E.J.[1], **Pegtel, D.M.**[2], **Grootjans, A.P.**[2] **& van der Veen, A.**[2]

[1]*Ministry of Agriculture, Nature Management and Fisheries, P.O. Box 30032, 9700 RM Groningen, The Netherlands; Fax +31 50 5992399; E-mail e.j.lammerts@lnvn.agro.nl;* [2]*Laboratory of Plant Ecology, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands; Fax +31 50 3632273*

Abstract. Basiphilous pioneer species are among the most endangered plant species in The Netherlands. They find most of their refuges in young coastal dune slacks, especially on the Wadden Sea islands. For the purpose of nature management it is important to know which processes control the presence of basiphilous pioneer communities, and to learn about the nature of slacks harbouring the concerning successional sequences.

In a large dune slack on the Island of Terschelling, we assessed soil nutrient status and tested for nutrient limitation in four chronosequential stages: 2, 6, 37 and ca. 80 yr of age. Stage 2 harboured a basiphilous pioneer vegetation; in the stages 3 and 4 a dense vegetation of dwarf shrubs and grasses occurred. Soil organic matter and nutrient concentrations in each stage were measured in 1991. In 1992 and 1993 fertilizers were applied to all stages to detect nutrient limitation. Rates of accumulation of organic matter, nutrients and above-ground biomass were estimated.

When interpreted as successional stages, the different stages represent a sequence as expected on the basis of general successional theory. There was a peak in yearly nutrient accumulation between the 6- and 37-yr old stage and a steady state after ca. 80 yr. Between the first two and the latter two stages a shift occurred from allogenic to autogenic succession which correlated with a shift in emphasis from available nutrients to light availability as limiting resources.

Basiphilous pioneer species suffered only deficiency of nitrogen, probably because of their low phosphorus requirements. It is concluded that in dune slack habitats, in addition to a low nutrient availability in general, a very low phosphorus availability favours basiphilous pioneer species to species showing co-limitation of nitrogen and phosphorus as found in some grasses and dwarf shrubs. A comparison between the effects of lime addition and the effects of nitrogen and phosphorus additions suggests that, in the early stages, soil buffering increases the availability of nitrogen and inhibits the availability of phosphorus.

Sod cutting is an effective technique for restoring basiphilous pioneer vegetation, when slacks are acidified only superficially and buffering-mechanisms can be reactivated. Yearly mowing and removing of standing crop may prolong the lifespan of basiphilous pioneer vegetation, when soil acidification has not yet dropped below pH 6.

Keywords: Acidification; Chronosequence; Nitrogen; Phosphorus; *Schoenus nigricans*.

Nomenclature: Phanerogams: van der Meijden (1990); Syntaxa: Schaminée et al. (1995).

Introduction

Many basiphilous pioneer species of hydroseres are endangered in The Netherlands and have become 'Red list' species. Most of their non-coastal habitats, such as fens and lowland brook valleys, have disappeared or are seriously degraded (Grootjans et al. 1988; van Wirdum 1991). In Dutch coastal areas, however, basiphilous pioneer communities with species such as *Dactylorhiza incarnata*, *Epipactis palustris*, *Liparis loeselii*, *Littorella uniflora*, *Parnassia palustris* and *Schoenus nigricans*, are still frequent, though declining, on almost bare sandy beach plains or blown-out calcareous slacks (van der Laan 1979; van Dijk & Grootjans 1993; Lammerts et al. 1995). Many of them are regional endemics (van der Maarel & van der Maarel-Versluys 1996). For the purposes of the conservation of rare species it is important to acquire knowledge of the environmental factors determining the rise and decline of these pioneer communities.

The basiphilous pioneer species build up typical basiphilous pioneer communities, such as the *Samolo-Littorelletum*, the *Centaurio-Saginetum* and the *Junco baltici-Schoenetum nigricantis*. They are, of course, rare as well and belong to the rarity category R5 (Izco 1998), i.e. with a small geographical range, low frequency of occurrence and relatively large local stands. They require a high pH (>6.0) and a low nutrient availability (e.g. Schat 1982; Rozema et al. 1985; Jones & Etherington 1992; Lammerts et al. 1995; van Beckhoven 1995; Ernst et al. 1996; Grootjans et al. 1996; Sival 1996). According to Tilman (1988), early successional species are competitively superior under conditions of high light and low availability of some soil resources (e.g. N), while late successional species can be characterized by the opposite conditions. In the dune slack Koegelwieck on the Dutch Wadden Sea island of Terschelling (Fig. 1) different stages of vegetation development are present at the same time. They result from sod cutting experiments having been executed during the last ca. 40 yr for the purpose of periodically regenerating pioneer stages. We compared the differences between these stages in ecosystem production and vegetation with some general features of succession

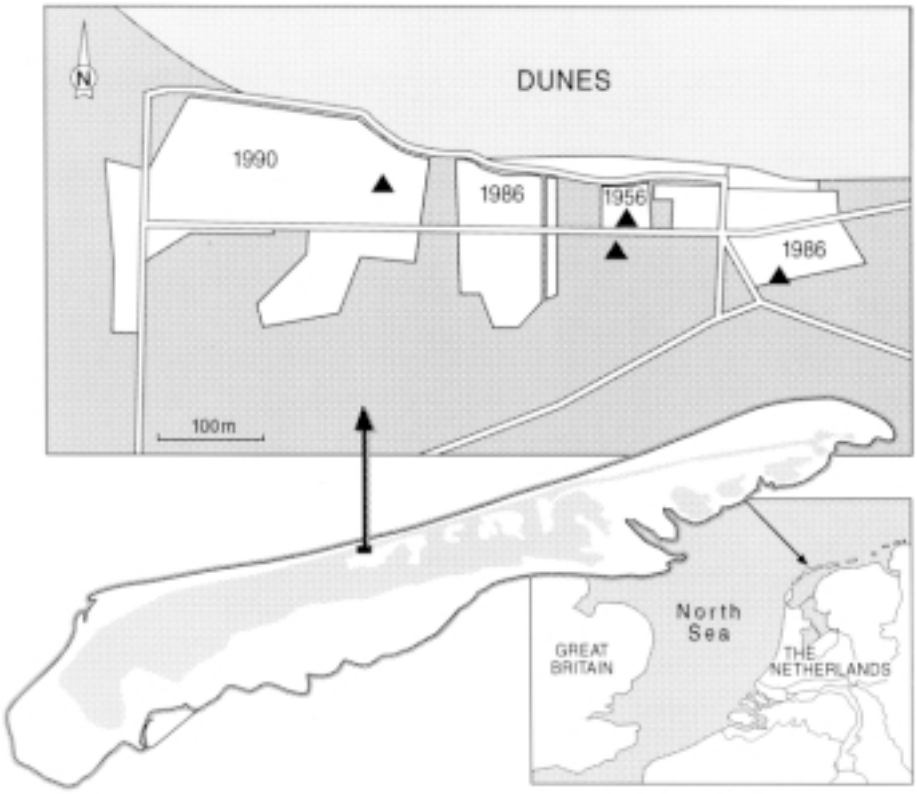

Fig. 1. The study site. The years of sod-cutting and the location of the fertilization experiments (▲) are indicated.

(Vitousek & Walker 1987; Chapin 1993) to identify the phase in dune slack succession in which basiphilous communities occur.

Furthermore, regarding the specific basiphilous character of dune slack habitats, we hypothesized that pH-dependent mechanisms (Rozema et al. 1985; Jones & Etherington 1992; Stuyfzand 1994; Ernst et al. 1996; Sival 1997; Lammerts et al. 1998) maintain a low nutrient availability by fixation of phosphates (Rorison 1960a; Clymo 1962; Etherington 1982). Low phosphorus requirements of *Carex flacca* (Willis 1963) and *Schoenus nigricans* (Ernst 1991) support this hypothesis. So does the observation that on late successional dune slack sites, where pioneer species have disappeared (Lammerts et al. 1995; Sival 1996), a large proportion of phosphorus (ca. 70 %) is organically bound. In this state its *availability* is considerably higher than on mineral soil, especially under anaerobic and acid conditions (Patrick & Khalid 1974). However, in most studies on nutrient limitation in dune slacks a primary N- and a secondary P-limitation is reported (Willis 1963; Dougherty et al. 1990; Olff et al. 1993; Lammerts & Grootjans 1997), probably because the general focus is on only one or two successional stages, neglecting the very early pioneer stages. We assume that the decline of basiphilous species in the course of dune slack succession, starting with a rapid accumulation of organic matter (personal observations in many dune slacks), is related to a shift from P- to N-limitation, at least to a decreasing P-limitation. This favours rapidly growing species which are efficient in capturing nutrients in the organic matter (cf. Odum 1969; Vitousek & Reiners 1975).

To specify the successional phase which harbours basiphilous pioneer vegetation and to test the hypotheses mentioned above, our investigations in the Koegelwieck focused on vegetation changes in relation to changes in buffering and nutrient status of the soil. Besides assessing the vegetation and site factors values, we carried out fertilization experiments in each of the stages. Nitrogen, phosphorus and potassium were added, both separately and in different combinations. Responses in above-ground biomass of total vegetation and species (groups) were recorded. Positive responses indicate which nutrients, through their shortage under natural conditions, hamper a rapid vegetation succession and thus give a competitive advantage to low-production pioneer species. In some plots $CaCO_3$ was added to introduce or reinforce buffering-mechanisms in a dune slack ecosystem. The results of these treatments, which are compared with the effects of nutrient additions, were expected to show the role of buffering mechanisms in controlling the nutrient status during dune slack succession.

Methods

The study area

The Koegelwieck is a large secondary dune slack (ca. 50 ha) on the Wadden Sea Island of Terschelling (53° 24′ N, 5°20′ E). It was formed as a blowout between 1825 and 1865 (van Dieren 1934). Sea water intrusions occurred up to about 1915. From then onwards the northern dune ridge has been carefully managed. Then, plant species of relatively fresh (ground-) water conditions colonized the mineral dune soil and vegetation succession began. Large-scale sod cutting experiments (covering areas of 0.5-20 ha) were carried out in 1956, 1959, 1986 and 1990. Fertilization experiments were performed in 1992 and 1993 in the cut areas as well as in an uncut area. The experimental sites were at least 100 m apart. Factors other than vegetation development, i.e. elevation, pedogenesis, distance from the coastline (in relation to salt deposition), and accessibility for grazing, were very similar.

Nutrient limitation was investigated in four chronosequential stages, where ca. 80, 37, 6 and 2 yr of vegetation development had taken place. Since about 80 yr ago, a relatively well-developed basiphilous pioneer vegetation has continuously been present somewhere in the slack (Westhoff 1947; Mörzer Bruijns 1951; State Forestry Service, unpublished data). Nowadays many of the basiphilous pioneer species are still well distributed over the area, though in small numbers.

Vegetation

The vegetation was recorded in plots of 2 m × 2 m using the decimal cover-abundance scale of Londo (1976). The data were transformed to percentage cover. Each seral stage was recorded in duplicate or triplicate.

Soil analysis

Soil sampling occurred in 1991 in triplicate close to the experimental sites. Samples were taken from the litter layer, the organic layer and the upper mineral layer. No organic layer was present in the 2-yr old stage, so the upper 5 cm and the 10 - 15 cm layer were sampled. The samples were analysed for pH-KCl (1 volume fresh soil with 5 volumes 1 mol/l KCl), organic matter content (ignition at 500 °C), $CaCO_3$-content (extraction for 2 h with 0.1n HCl), total nitrogen (digestion with phenol-H_2SO_4 + Se and colorometric analysis of NH_3 using endophenol blue with salicylate), soluble phosphates and total phosphorus (respectively colorometric analysis of PO_4^{3-} using ammonium molybdate after mixing with water for 22 h and digestion with H_2SO_4 + HNO_3) and total potassium (using a flame atomic adsorption spectrometer, AAS). Bulk density was determined by weighing 100 cc. dry soil samples.

Fertilization experiments

Nitrogen, phosphorus and potassium were added to the experimental sites in different combinations. Slow release fertilizer granules (brand 'Osmocote') were used; they release nutrients in the course of 4-6 months: urea (39 % w/w N), calcium biphosphate (17% w/w P) and potassium sulphate (37% w/w K). Quantities of 16 g/m^2 N, 16 g/m^2 P and 16 g/m^2 K were used. Liming was done by adding 300 g/m^2 $CaCO_3$.

The experimental design involved 10 treatments: N, P, K, NP, NK, PK, NPK, $CaCO_3$, $CaCO_3$+NPK and C (= Control, i.e. no addition of any nutrient). The fertilizer was added at the start of the growing seasons (the beginning of May) in 1992 and 1993. The experimental sites in each of the four successional stages consisted of plots of 1 m × 1.5 m with five replicates for each treatment. All plots were arranged in a randomized block design. Strips of 0.5 m were left untreated between the plots to prevent interactions. At the end of the growing season (September) the total above-ground standing crop was harvested from each plot, each year in a different strip of 0.2 m × 1 m. In 1992 the fertilization experiment on the 37-yr sites was disturbed by the picking of cranberry (*Vaccinium macrocarpos*) just before harvesting had been planned. In 1993 the 2-yr plots could not be harvested because the experimental site was inundated. After drying for at least 48 h at 70°C, the biomass of each species (group) was weighed. In 1993 only total biomass was weighed in the fertilization experiment in the 6-yr old stage.

Data analysis

All means reported for soil factors and above-ground biomass are based on untransformed data.

Univariate one-way analyses of variance, using the Tukey multiple comparison test, were applied to detect differences in soil factors between sample sites and to test differences in natural above-ground biomass between successional stages.

Overall effects of nutrients and lime additions were tested per successional stage in two different designs: a nutrient-design, concerning the addition of nitrogen, phosphorus and potassium, separately and in all possible combinations, and a lime design, concerning the addition of $CaCO_3$ with and without a full nutritional supply of NPK. The effects on above-ground biomass were tested with three- and two-factor univariate

analyses of variance (ANOVA). The effects on all species present, considered simultaneously, were compared with three- and two-factor multivariate analyses of variance (MANOVA) using Pillai's multivariate test. A multivariate analysis was only executed when the responses of individual species were interdependent (tested with the Bartlett test of sphericity at a significance level of 0.05). Significant main effects of the additions of nutrients or lime, according to the multivariate analyses, indicate shifts in proportional biomass of the species present. Univariate tests for each species separately, with and without taking all other species as covariates (on the basis of a preceding covariance analysis), show which species is (are) responsible for these shifts.

Results

Vegetation

Vegetation in the 2-yr old stage was sparse (Table 1). The cover of ca. 25% was mainly built up by *Juncus* species.

In the 6-yr old stage, *Schoenus nigricans* was the dominant species. Total cover was ca. 60-70%. Many species had colonized the area, among which were several small *Littorellion* species. Except for *S. nigricans* itself, few species of the plant community *Junco baltici-Schoenetum nigricantis* were present in the herb layer. Several characteristic moss species, however, did occur in the vegetation, e.g. *Campylium stellatum* and *Drepanocladus aduncus*.

In the 37-yr old stage *S. nigricans* and other basiphilous pioneer species, the mosses included, had almost completely disappeared. Dwarf shrubs, mainly *Oxycoccus macrocarpos*, *Erica tetralix* and *Salix repens*, dominated this stage. These species produce a thick litter layer.

In the ca. 80-yr old stage *Calamagrostis epigejos* had formed a tall layer above the dwarf shrubs. *Erica tetralix* had disappeared, but dense *Salix repens* vegetation was still present below the *C. epigejos* layer. *Oxycoccus macrocarpos* appeared to languish in these circumstances, though this species still was very vigorous in some other sites in the slack. This stage was characterized by tall vegetation with a very small number of species.

Table 1. Floristic composition of the vegetation on experimental sites. Analyses were made in 1992 with the decimal scale of Londo (1976); data are transformed to mean % cover.

Age	2 yr	6 yr	37 yr	c. 80 yr
No. of analyses (*n*)	3	2	2	2
Juncus alpinoarticulatus	9	2	1	
Juncus articulatus	9	1		
Samolus valerandi	1	0.5		
Carex oederi	1	1		
Potentilla anserina	1	1	5	2
Hydrocotyle vulgaris	1	3	0.5	0.5
Mentha aquatica	1	1		
Salix repens	1	4	5	7
Glaux maritima	0.7			
Taraxacum officinale	0.7			
Ranunculus flammula	0.7	1	0.5	
Agrostis stolonifera	0.7	3		
Lythrum salicaria	0.3	3	4	0.5
Trifolium pratense	0.3			
Schoenus nigricans		20		
Centaurium littorale		1		
Sagina procumbens		1		
Carex flacca		1	0.5	
Hippophae rhamnoides		1		
Ranunculus repens		1		
Galium palustre		1		
Ophioglossum vulgatum		1		
Calamagrostis epigejos		1	5	15
Littorella uniflora		0.5		
Radiola linoides		0.5		
Linum catharticum		0.5		
Equisetum palustre		0.5		
Dactylorhiza incarnata		0.5		
Agrostis canina		0.5		
Leontodon hispidus		0.5		
Plantago major		0.5		
Carex arenaria		0.5	0.5	
Prunella vulgaris		0.5		
Carex panicea		0.5		
Empetrum nigrum		0.5		
Carex trinervis		0.5	1	0.5
Oxycoccus macrocarpos		0.5	75	65
Erica tetralix			15	
Lotus corniculatus			3	
Epipactis palustris			1	
Phragmites australis			1	
Potentilla erecta			0.5	
Rhinanthus minor			0.5	
Trifolium repens			0.5	
Moss layer		15	0.5	
Total cover	25	65	> 95	>95

Soil

The mineral soil in all successional stages was decalcified (Table 2). Below the oldest two stages (37 and ca. 80 yr) the pH-KCL values in the mineral layers were accordingly low (4.7-4.9). In the litter and the organic top layer of these stages (containing ca. 70% and ca. 20 % organic matter, respectively) some carbonate (not necessarily calcium carbonate) was detected. The pH-values in the litter layer (to a maximum depth of 1 cm) of the oldest stages reached values up to somewhere between 5.7 and 5.9 and declined again to 4.5-4.7 in the organic layer immediately below the litter. In the mineral top layer of the 2-yr old stage the pH reached neutral values around 7.0. The underlying mineral layer (at a depth of 10-15 cm) showed a pH of 5.2, close to the values found in the mineral layers below the oldest stages, though probably having increased somewhat after sod-

Table 2. Soil characteristics of experimental sites. The following soil layers are distinguished : O = litter layer; A = the humic layer; C = mineral layer below A; C* = as C, but at the surface (one year after sod cutting). The values are means of samples taken in triplicate in 1991. Significance levels for the differences in mean values between the different stages and soil layers are given by the characters in superscript; mean values without superscript character in common differ significantly (p <0.05) according to the Tukey multiple comparison test.

Stage	Layer	Depth (cm)	pH-KCl	Organic matter (%)	N-total (%)	P-H_2O (mg/100g)	P-total (mg/100g)	K-total (mg/100g)	$CaCO_3$ (%)
2-yr	C*	0-5	7.0 ^{e}	0.5 a	0.01 ^{a}	0.04 ^{a}	4.9 ^{a}	6.5 ^{a}	<0.1 ^{a}
2-yr	C	10-15	5.2 ^{bc}	0.5 ^{a}	0.02 ^{a}				<0.1 ^{a}
6-yr	A	0-2	6.4 ^{de}	7.3 ^{ab}	0.18 ^{b}	0.61 ^{a}	17.6 ^{b}	8.1 ^{a}	<0.1 ^{a}
6-yr	C	10-15	6.9 ^{e}	0.3 ^{a}	0.00 ^{a}				<0.1 ^{a}
37-yr	O	0-0.5	5.9 ^{cd}	74.2 ^{d}	0.91 ^{d}		66.5 ^{c}	50.4 ^{b}	0.2 ^{a}
37-yr	A	0.5-7	4.5 ^{a}	19.6 ^{c}	0.32 ^{c}	6.01 ^{b}	25.2 ^{b}	17.6 ^{a}	0.1 ^{a}
37-yr	C	10-15	4.9 ^{ab}	0.5 ^{a}	0.00 ^{a}				<0.1 ^{a}
80-yr	O	0-1	5.7 ^{c}	71.7 ^{d}	0.99 ^{e}		75.7 ^{c}	57.5 ^{b}	0.4 ^{a}
80-yr	A	1-10	4.7 ^{ab}	18.2 ^{bc}	0.24 ^{b}	3.06 ^{ab}	27.1 ^{b}	14.7 ^{a}	0.2 ^{a}
80-yr	C	15-20	4.7 ^{ab}	0.6 ^{a}	0.02 ^{a}				<0.1 ^{a}

cutting. In the 6-yr old stage in this same layer the pH had increased further to 6.9. The 2 cm organic top layer in this stage (containing ca. 7% organic matter) showed a decrease in pH to 6.4. This decrease may continue till the pH reaches values as measured in the organic layers of the oldest stages.

Organic matter content and nitrogen, phosphorus and potassium concentrations in the top layers of the different stages showed similar patterns (Table 2). The 2-yr old stage gave the lowest figures, the 6-yr old stage showed intermediate values and high concentrations were found in the organic and the litter layers of the oldest stages. Especially the amount of soluble phosphates was significantly larger in the third stage than in the previous stages. Hardly any nitrogen could be detected in the mineral subsoil.

Fertilization experiments in four successional stages

A general picture

A univariate analysis of variance indicated significant differences in total above-ground biomass in Control plots between the younger two stages (ca. 50 and 150 g/m^2 in respectively the 2- and 6-yr old stage, cf. Table 3) and each of the elder two stages (ca. 1500 g/m^2 in the 37-yr old stage and ca. 800 g/m^2 in the ca. 80-yr old stage). The difference between the latter two was also significant. For the 6- and ca. 80-yr old stages, all experimental results in 1992 and 1993 were very similar (Tables 3, 4 and 5).

The effects of nutrient addition

In the 2-yr old stage, main effects of nitrogen and phosphorus addition on biomass production were clear (Table 4). The dominant species *Juncus alpinoarticulatus* increased by separate addition of both nitrogen and phosphorus (Tables 3 and 4). Phosphorus addition caused an increase in biomass of the small group of 'other' species, i.e. all species which could not be distinguished in the biomass analysis (cf. Tables 1 and 3). The combined addition of N and P gave a higher yield of *Juncus alpinoarticulatus* biomass only up to the level which may be expected from the effects of the separate supplies: the N×P interaction was not significant (Table 4).

In the 6-yr old stage, total biomass increased after nitrogen addition, while no effect of phosphorus addition on total biomass was found (Table 4). However, phosphorus addition, alone and when combined with nitrogen addition, led to shifts in the proportional biomass of species (Table 4). The positive effects of phosphorus addition on *Calamagrostis epigejos*, *Salix repens* and *Agrostis stolonifera* were mainly responsible for these results (Tables 3 and 4). The addition of nitrogen alone led to biomass increases of *Juncus alpinoarticulatus*, *Calamagrostis epigejos*, *Oxycoccus macrocarpos*, some *Carex* spp. and the group of other species (many basiphilous pioneer species, cf. Table 1).

In the 37-yr old stage a main effect of nitrogen addition on total biomass and on *C. epigejos* and *O. macrocarpos* biomass was detected. The addition of phosphorus alone caused a larger biomass production of other species (Tables 3 and 4). The multivariate analyses showed that responses of individual species did not lead to significant shifts in proportional biomass (Table 4).

In the ca. 80-yr old stage, nitrogen addition increased total biomass production only in 1992. In 1992 and 1993, however, nitrogen addition caused changes in the proportional biomass of occurring species. This response was caused by positive effects on *C. epigejos* and, in 1992, on *Carex* species (here *C. trinervis*, see Table 1). *Carex trinervis* also increased with the addition of phosphorus, especially when applied together with nitrogen.

Table 3. Biomass of the vegetation and constituent species (g/m^2) in all stages after performing the experiments in 1992 and 1993. Mean values and population standard deviations of five replicates are given. The treatment 'lime' represents $CaCO_3$-addition, the treatment 'lime*' represents the combined addition of $CaCO_3$ and NPK. A.sto. = *Agrostis stolonifera*; C.ep. = *Calamagrostis epigejos*; C.sp. = *Carex* species; E.tet. = *Erica tetralix*; J.alp. = *Juncus alpinoarticulatus*; J.art. = *Juncus articulatus*; O.m. = *Oxycoccus macrocarpos*; S.nig. = *Schoenus nigricans*; S.rep. = *Salix repens*.

2-yr (1992)	J.art.	s.d.	J.alp.	s.d.	Other	s.d.	Total	s.d.
C	22,0	19,9	29,3	19,1	2,6	2,3	53,9	17,9
N	10,6	18,3	101,6	91,9	3,1	2,9	115,3	102,6
P	14,4	24,5	103,9	59,1	8,1	11,2	126,4	67,1
K	6,4	6,7	36,3	20,1	1,3	0,9	44,0	21,0
NP	31,4	54,5	151,4	142,8	24,2	31,5	206,9	138,4
NK	11,2	12,7	86,5	76,7	3,9	2,0	101,5	71,0
PK	7,9	5,3	84,1	47,7	18,6	24,4	110,6	70,0
NPK	36,2	33,3	300,0	177,7	20,7	25,0	356,9	194,1
Lime	16,4	16,4	65,1	43,6	13,7	18,1	95,1	47,4
Lime*	18,9	23,3	145,8	72,1	40,8	32,4	205,4	57,0

6-yr (1992)	J.alp.	s.d.	S.nig.	s.d.	C.ep.	s.d.	O.m.	s.d.	S.rep.	s.d.	C.sp.	s.d.	A.sto.	s.d.	Other	s.d.	Total	s.d.
C	9,5	6,7	96,8	95,8	3,7	4,2	0,4	0,7	10,0	18,0	4,4	3,1	6,7	4,7	15,5	7,3	146,9	118,3
N	40,4	21,6	91,7	103,5	14,7	21,9	4,9	6,7	25,2	13,3	34,9	27,4	17,4	12,1	78,3	25,2	307,4	78,0
P	29,7	17,5	14,2	11,9	17,6	14,4	6,9	9,3	21,8	19,4	3,8	0,9	3,0	4,2	24,2	22,8	121,0	73,6
K	28,7	10,5	93,6	88,2	5,8	5,6	0,0	0,0	18,4	25,0	3,3	2,9	5,2	5,6	9,6	7,8	164,5	119,1
NP	40,3	9,8	74,1	76,6	57,9	96,2	4,2	5,4	51,6	46,6	18,2	14,0	68,8	45,9	59,8	34,8	374,8	106,2
NK	24,9	13,3	80,7	80,1	25,7	27,0	10,7	22,1	7,8	6,4	34,8	30,9	11,0	11,5	52,0	46,5	247,6	143,3
PK	26,6	11,5	39,7	38,7	4,8	3,8	3,2	3,6	74,3	66,5	9,4	17,8	6,5	7,7	47,0	33,8	211,6	126,6
NPK	35,8	15,5	150,9	120,8	78,1	108,7	0,1	0,2	9,6	14,5	13,3	13,6	95,1	99,8	58,6	24,0	441,5	154,5
Lime	15,8	6,8	29,3	29,5	12,5	17,9	14,0	20,4	138,6	155,1	19,9	21,6	5,7	5,8	74,3	72,9	310,1	251,1
Lime*	17,5	4,6	95,7	122,3	14,6	17,0	3,7	3,3	57,3	42,7	10,8	2,5	34,2	27,2	200,2	176,1	434,2	144,8

6-yr (1993)	Total	s.d.
C	131,1	149,9
N	381,0	161,7
P	24,0	9,4
K	70,0	89,2
NP	235,6	120,0
NK	178,6	101,5
PK	40,8	29,3
NPK	217,3	109,5
Lime	83,6	52,4
Lime*	317,8	104,5

37-yr (1993)	C.ep.	s.d.	O.m.	s.d.	S.rep.	s.d.	E.tet.	s.d.	Other	s.d.	Total	s.d.
C	76,4	53,0	949,1	266,8	55,2	32,5	275,7	154,2	81,4	13,3	1437,8	290,9
N	203,7	78,8	871,6	115,3	30,7	17,3	106,5	78,6	53,6	35,9	1266,0	82,3
P	204,2	343,1	696,8	283,9	49,0	46,0	167,1	121,4	118,4	104,5	1235,5	247,3
K	61,5	10,9	993,0	126,9	42,5	13,4	145,2	88,9	48,7	23,3	1290,9	126,6
NP	137,9	72,8	933,8	285,3	65,4	29,2	183,2	195,6	151,1	71,8	1471,5	190,3
NK	150,6	15,9	976,3	259,7	59,9	14,6	311,1	260,8	110,8	32,8	1608,7	166,9
PK	38,8	19,4	611,3	229,1	47,6	25,0	379,7	130,6	80,7	48,0	1158,2	186,5
NPK	138,0	49,5	1041,9	291,8	63,6	27,9	203,8	226,8	132,2	71,0	1579,5	175,3
Lime	125,0	159,1	717,7	142,7	71,6	38,4	214,6	234,1	59,4	16,7	1188,2	189,2
Lime*	124,1	44,5	820,6	124,9	73,9	64,9	80,6	161,2	60,4	27,0	1159,6	121,4

80-yr (1992)	C.ep.	s.d.	O.m.	s.d.	S.rep.	s.d.	C.sp.	s.d.	Other	s.d.	Total	s.d.
C	156,1	37,6	233,6	111,7	269,9	176,7	49,4	33,6	83,6	36,9	792,7	254,8
N	225,0	93,0	239,8	150,1	214,6	33,9	29,3	30,2	84,3	48,4	793,0	223,7
P	103,0	36,2	291,0	207,4	279,3	122,3	48,1	43,4	74,8	9,2	796,2	51,0
K	187,3	106,2	185,8	121,1	320,8	149,5	44,4	30,0	64,1	26,5	802,4	200,0
NP	297,7	91,6	348,2	110,8	191,3	106,3	63,2	47,8	93,6	59,0	993,9	133,0
NK	337,3	101,9	258,5	182,2	329,8	202,4	21,1	15,7	95,2	46,2	1041,9	231,6
PK	127,5	67,5	180,9	34,8	295,6	150,4	18,8	18,3	57,2	9,6	680,0	160,3
NPK	254,6	100,2	230,7	136,9	367,2	185,1	135,3	83,1	95,9	38,9	1083,6	169,6
Lime	150,4	72,3	325,4	123,2	439,5	192,6	46,6	43,1	72,7	38,9	1034,5	211,8
Lime*	247,7	87,8	336,8	99,4	273,5	107,1	51,2	33,1	88,6	61,7	997,7	83,9

80-yr (1993)	C.ep.	s.d.	O.m.	s.d.	S.rep.	s.d.	Other	s.d.	Total	s.d.
C	129,5	19,6	308,9	132,7	244,6	56,9	117,5	111,2	800,5	240,0
N	314,0	127,0	288,4	177,0	181,4	24,4	146,7	61,5	930,6	175,0
P	106,8	61,5	314,1	313,0	286,6	160,8	125,1	94,3	832,6	377,4
K	144,5	70,7	189,3	146,4	267,0	193,8	151,7	201,7	752,6	347,7
NP	300,1	65,9	293,7	148,4	215,9	175,6	154,6	44,2	964,3	52,3
NK	345,8	121,4	238,4	137,2	260,0	161,4	143,5	92,5	987,7	177,1
PK	114,1	36,6	286,6	154,5	469,2	257,3	121,0	109,8	990,8	336,1
NPK	301,7	86,0	156,4	142,0	371,0	241,0	108,2	19,1	937,3	301,3
Lime	150,6	92,5	340,1	176,1	419,2	415,0	137,5	44,4	1047,4	391,9
Lime*	236,5	72,8	293,6	113,3	154,9	63,1	105,2	38,0	790,2	222,0

Table 4. Test results for the effects of nutrient addition. The significances of the main effects on total and species biomass of the addition of each nutrient and of their interactions are given as an outcome of the application of a 3-way ANOVA. Symbols in bracket point to cases where results for a species are only significant if all other species are taken as covariates. The significance of changes in vegetation composition results from applying a 3-way MANOVA on the effects of nutrient addition on all species (groups) simultaneously. Test results are given as - =not significant; * = p <0.05; ** =p <0.01; *** =p <0.001.

	2 yr- stage							6 yr-stage							37 yr-stage							ca. 80-yr stage						
	N	P	K	NxP	NxK	PxK	NxPxK	N	P	K	NxP	NxK	PxK	NxPxK	N	P	K	NxP	NxK	PxK	NxPxK	N	P	K	NxP	NxK	PxK	NxPxK
Results 1992																												
Total biomass	**	**	-	-	-	-	-	***	-	-	-	-	-	-								**	-	-	-	-	-	-
Vegetation composition	**	**	-	-	-	-	-	***	**	-	**	-	-	-								***	-	-	*	-	-	-
Juncus articulatus	-	-	-	-	-	-	-																					
Juncus alpinoarticulatus	**	**	-	-	-	-	-	*	-	-	-	-	-	(*)														
Schoenus nigricans								-	-	-	-	-	-	-														
Calamagrostis epigejos								(***)	(**)	-	(**)	-	-	-								***	-	-	-	-	-	-
Oxycoccus macrocarpos								(*)	-	-	-	-	-	-								-	-	-	-	-	-	-
Salix repens								-	*	-	-	**	-	-								-	-	-	-	-	-	-
Carex spec.								**	-	-	-	-	-	-								(*)	*	-	**	-	-	-
Agrostis stolonifera								**	*	-	*	-	-	-														
Other species	-	**	-	-	-	-	-	***	-	-	-	-	-	-								-	-	-	-	-	-	-
Results 1993																												
Total biomass								***	-	-	-	-	-	-	**	-	-	-	*	-	-	-	-	-	-	-	-	-
Vegetation composition															-	-	-	-	-	-	-	***	-	-	-	-	-	-
Calamagrostis epigejos															(*)	-	-	-	-	-	-	***	-	-	-	-	-	-
Oxycoccus macrocarpos															(*)	-	-	*	-	-	-	-	-	-	-	-	-	-
Salix repens															-	-	-	-	-	-	-	-	-	-	-	-	-	-
Erica tetralix															-	-	-	-	-	-	*							
Other species															-	*	-	-	-	-	-	-	-	-	-	-	-	-

The effects of lime addition

In the 2-yr old stage the addition of only lime had no effect on biomass production (Table 5). An increase in biomass of *Juncus alpinoarticulatus* occurred after joint addition of lime and NPK, but this increase was much larger after addition of only NPK (Table 3). A multivariate analysis was not carried out here, because, according to Bartlett test of sphericity, the effects on the vegetation components were not interdependent.

In the 6-yr old stage, the addition of lime did not cause a change in total biomass production (Table 5). The relative biomass of composing species was influenced by the separate additions of lime and NPK as well as by their interaction, when added together (Table 5). *Juncus alpinoarticulatus* and *Calamagrostis epigejos* biomass

Table 5. Test results for the effects of lime addition. The main effects of the addition of lime and nutrients (a complete gift of N, P and K) were considered by comparing control plots with plots where $CaCO_3$, NPK and $CaCO_3$ +NPK were added. For further exp lanations see Table 4 (here a 2-way ANOVA and a 2-way MANOVA were used).

	2-yr stage			6-yr stage			37-yr stage			80-yr stage		
	NxPxK	Lime	NPK × Lime	NPK	Lime	NPK × Lime	NPK	Lime	NPK × Lime	NPK	Lime	NPK × Lime
Results 1992												
Total biomass	***	-	-	*	-	-				-	-	-
Vegetation composition				**	*	**						
Juncus articulatus	-	-	-									
Juncus alpinoarticulatus	**	-	*	**	(*)	*						
Schoenus nigricans				-	-	-						
Calamagrostis epigejos				(**)	(**)	(**)				*	-	-
Oxycoccus macrocarpos				-	-	-				(*)	-	-
Salix repens				-	*	-				-	-	-
Carex species				-	-	-				(**)	-	-
Agrostis stolonifera				*	-	-						
Other species	*	-	-	-	*	-				-	-	-
Results 1993												
Total biomass				*	-	-	-	**	-	-	-	-
Vegetation composition										**	-	-
Calamagrostis epigejos							-	-	-	**	-	-
Oxycoccus macrocarpos							-	(**)	-	-	-	-
Salix repens							-	-	-	-	-	-
Erica tetralix							-	-	-			
Other species							-	*	-	-	-	-

Table 6. Yearly increase in organic matter and macronutrients in the soil compartment and of above-ground biomass in the periods between the chronosequential stages. All data are expressed in g/m^2/yr.

Period	2 - 6 yr	6 - 37 yr	37 - 80 yr
Organic matter	256	271	99
N-total	6.56	3.97	0.67
P-total	– 0.11	0.29	0.19
K-total	– 0.87	0.23	0.06
Biomass	23	42	– 15

increased after both lime addition and NPK addition (Tables 3 and 5). When added up, the biomass of these species did increase less than expected on the basis of the separate additions (Table 3), thus indicating a significant interaction between both treatments in relation to these species (Table 5). *Salix repens* and the group of other species produced significantly more biomass after lime addition (Tables 3 and 5).

In the 37-yr old stage, lime addition significantly reduced total biomass production (Tables 3 and 5), especially of *Oxycoccus macrocarpos*, the dominant species, and of the group of other species (Table 5). No multivariate analysis was carried out here because of the lack of interdependence between species.

In the ca. 80-yr old stage, addition of $CaCO_3$ showed no significant effects on total biomass or on the biomass of individual species (Table 5).

Changes in soil organic matter, nutrient pools and biomass production

The chronosequence in the Koegelwieck showed a coherent set of directional changes in the soil compartment (Fig. 2). Accumulation of organic matter clearly coincided with increasing pools of nitrogen, phosphorus and potassium, probably causing the simultaneous increases in above-ground biomass, at least until the third stage. However, organic matter and nutrient pools did not accumulate synchronously. Table 6 shows that the organic matter content of the top layer increased at about the same average speed between the 2- and 6-yr old stage as between the 6- and 37-yr old stage; accumulation slowed down between the 37- and ca. 80-yr old stage. The average rate of increase of the nitrogen pool was largest until the 6-yr old stage, declining sharply after the 37-yr old stage. Phosphorus and potassium started to accumulate well after the 6-yr old stage; the average growth speeds of their pools slowed down again after the 37-yr old stage. The average net yearly production of above-ground biomass was largest between the 6- and 37-yr old stage but was negative after the 37-yr old stage.

Discussion

The Koegelwieck sod-cutting experiments can only be interpreted as successional phases if they have experienced largely similar abiotic conditions in the pioneer phase and similar environmental influences during their further development. All cut areas are located at about the same distance from the coastline and adjacent dunes. Their altitude and mineral soil conditions are very similar. Their histories, of course, are somewhat different because the development of each stage covers different periods of the 20th century. In the whole of the last century the area was rather stable, geomorphologically and otherwise. Only nitrogen availability may have been smaller in the earlier cut stages than in the latter ones due to an increasing atmospheric deposition of nitrogen compounds. We assume that this effect led to only small differences in successional speed, because atmospheric deposition is still relatively small compared to the mainland (Sival 1997). Therefore we conclude that the chronosequence represents ca. 80 yr of succession.

Oxycoccus macrocarpos, being dominantly present in the older stages, is a neophytic species, unintentionally introduced on the island of Terschelling around 1840 (Van Dieren 1934). It nowadays establishes and spreads spontaneously throughout dune slacks on the Islands of Terschelling and Vlieland. Therefore we consider the species as a natural element in this century's dune slack succession.

Ecosystem succession and vegetation change

Successional change in ecosystem production in the Koegelwieck seems to fit the general scheme of Vitousek & Reiners (1975) describing the relation between nutrient retention and ecosystem succession: a normal curve skewed with a peak in the early stages. A complete picture for the Koegelwieck is not available because of the lack of data on below-ground biomass and plant tissue nutrient concentrations. However, the available data on net above-ground biomass production and on the development of soil nutrient pools (Table 6) show a fast increasing net ecosystem production in the beginning, peaking between the 6- and 37-yr old stage, and gradually decreasing until a steady state is reached in the oldest stage (cf. Gorham et al. 1979). Basiphilous pioneer vegetation only occurs in the early two stages of increasing net ecosystem production and has disappeared before net ecosystem production has reached its peak. The actual organic matter content of the soil was low and nutrient pools were small in the early two stages, increasing relatively fast between the second and third phase (Fig. 2).

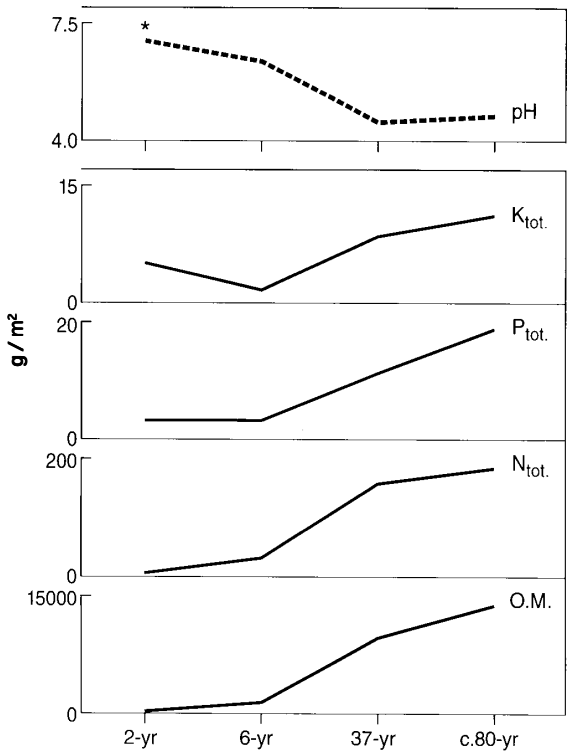

Fig. 2. Changes in soils in the Koegelwieck chronosequence. O.M. = organic matter; $N_{tot.}$ = total nitrogen content; $P_{tot.}$ = total phosphorus content; $K_{tot.}$ = total potassium content. pH is measured in the organic top layer. The pH-value in the 2-yr stage, marked by an asterisk, is in fact measured in a mineral soil sample because no organic matter was present yet.

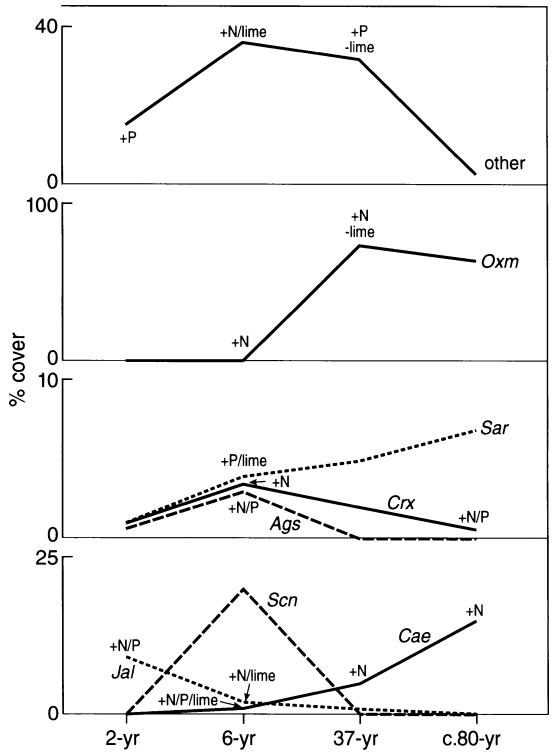

Fig. 3. Abundance changes of plant species (groups) in the Koegelwieck chronosequence. Cae = *Calamagrostis epigejos*; Jal = *Juncus alpinoarticulatus*; Scn = *Schoenus nigricans*; Ags = *Agrostis stolonifera*; Crx = *Carex* spp; Sar = *Salix repens*; Oxm = *Oxycoccus macrocarpos*; other species, see Table 1. Significant changes (p <0.05) in productivity, caused by the fertilization experiments, are denoted above or below the graphs by + (biomass increase) or – (biomass decrease) followed by the minerals involved (interactions not indicated).

The fertilization experiments indicated that both nitrogen and phosphorus limit biomass production in the first two stages. In the latter two stages P-limitation plays only a minor role. N-addition still led to increasing biomass production. Simultaneous vegetation change was characterized by a replacement of annuals, rosette plants and low productive perennials (*Schoenus nigricans* and a few small *Carex* and *Juncus* species) by dwarf shrubs as *Oxycoccus macrocarpos* and *Erica tetralix* and/or high productive grasses as *Calamagrostis epigejos*. The species from the first two phases, compared to the species of the older phases, have physiological traits advantageous in early primary succession, such as small seeds and a high relative growth rate by investing in productive tissue (Chapin 1993). The species of the older stages mainly invest in supportive, non-productive tissue lifting their photosynthetically active parts to the top layer of the vegetation. This change in physiological traits represents a shift from allogenic to autogenic succession, i.e. from succession controlled mainly by environmental factors (e.g. soil nutrient status) to succession mainly controlled by vegetation processes as competition and facilitation (van Andel et al. 1993). This shift is correlated with a shift in limiting resources from nutrients to light as may be expected in the course of successional change (Tilman 1988, 1990).

The nature of the dune slack environment

The specific dune slack conditions determining the rise, presence and decline of *basiphilous* pioneer vegetation can be inferred from differences in species composition between stages and, in the fertilization experiments, from differences in responses of different species and of the same species in different stages (Fig. 3).

Co-limitation of N and P applied to the dominant species in the first stage and to grasses in the second stage. In the second stage, however, N-addition alone and not P-addition led to an increasing production of total biomass and of the biomass of *Carex* species (*C. flacca* and *C. oederi* in this phase) and the group of other species (including many characteristic basiphilous species). Willis (1963) also found a clear limitation of only

nitrogen for small *Juncus* and *Carex* species in dune slacks. He found a small phosphorus requirement for *Carex flacca*. If this is true for more small pioneer species known to be basiphilous, a strong phosphorus deficiency may be crucial for a longer maintenance of *Caricion davallianae* vegetation by inhibiting vigorous growth of grasses. The observation of a large increase of readily available, water-soluble phosphates in the soil between the second and third stage (Table 2) supports this view.

The low nutrient requirement of *Schoenus nigricans* (Ernst 1991; van Beckhoven 1995) also fits this description. The fertilization experiments, however, did not reveal any nutrient limitation at all for *Schoenus nigricans*. This may be due to its low relative growth rate (Boatman 1972; Grime & Hunt 1975) and to its ability to release oxygen from the roots under waterlogged conditions (Schat 1982; Ernst & van der Ham 1988; van Beckhoven 1995), also known from several other wetland pioneer species with well developed aerenchyma (Armstrong 1982). This oxygen loss may, in a calcareous environment, lead to a rapid decomposition of organic matter (cf. Roelofs et al. 1984, reporting on *Littorella uniflora*), under which conditions nitrification on a very local scale and, further away from the roots, denitrification occurs (Reddy & Patrick 1984; Engelaar 1994). In this way *Schoenus nigricans* probably fulfils its own nitrogen requirements under nutrient-poor conditions and at the same time stabilizes a nutrient-poor pioneer phase for other basiphilous species.

A possible role of buffering mechanisms in maintaining N and P co-limitation in dune slacks appears from the results of the addition experiments with lime. The biomass of *Juncus alpinoarticulatus* and the group of 'other' species in the 6-yr old stage, both limited by nitrogen only, increased after lime addition (Fig. 3), just as expected. A rise in pH is known to reinforce nitrogen mineralization, more precisely nitrification (Etherington 1982). The group of other species in the 37-yr old stage (mainly consisting of *Lythrum salicaria*, *Potentilla anserina* and *Lotus corniculatus*) showed a decrease in biomass after lime addition as was expected for phosphorus-limited species. In the presence of lime, up to 50% of the inorganic phosphorus may be fixed in mineral phosphates (Etherington 1982). The observed response of phosphorus-limited species may be interpreted as the opposite effect of the rapid growth these species show after acidification of the habitat. This also explains the biomass decrease of *Oxycoccus macrocarpos* after lime addition in the 37-yr old stage, though this species only showed a secondary phosphorus limitation here (Tables 3 and 4). The significant NPK × $CaCO_3$ interactions (Table 5), resulting in a decrease in biomass production of *Juncus alpinoarticulatus* and *Calamagrostis epigejos* in the first two stages (Table 3), also confirm the idea that a high pH causes phosphorus limitation: the excessive biomass production after NPK-addition decreased after additional lime addition, possibly because of a decreasing phosphorus availability.

Other effects of the addition of $CaCO_3$, e.g. the nutritional effects of mineral calcium (Clymo 1962; Rorison 1960a, b), can also play a role, but generally they cannot be distinguished from the mechanisms mentioned above. The response of *Salix repens* in the 6-yr old stage, however, may be understood as such, i.e. the biomass of this species, though showing phosphorus limitation, increased significantly after lime addition.

Our results stress the importance of phosphorus (co-)limitation in early phases, suggesting a relation with pH-buffering. As such they may be considered to reinforce the idea that buffering mechanisms make dune slack environments very suitable habitats for basiphilous pioneer vegetation (cf. Sival et al. 1997). The life span of such communities in dune slacks is relatively short, certainly when compared to stable fen habitats (Boyer & Wheeler 1989; van Wirdum 1993). There are, however, differences between dune slack types depending on differences in active buffering-mechanisms and in speed of organic matter accumulation (Lammerts & Grootjans 1998).

Consequences for nature management

Maintaining suitable conditions for basiphilous pioneer species in dune slacks implies the maintenance of N and P co-limitation, especially of P-limitation. A low amount of accumulated organic matter and a soil pH > 6.0 appear to be crucial in this respect. When, by natural causes or otherwise, these conditions have disappeared, basiphilous pioneer vegetation can be restored by sod-cutting, at least when buffering mechanisms are able to raise low soil-pH values to neutral or basic again. Sod-cutting appears to be effective not only in the Koegelwieck but also in other slacks on the Wadden Sea Islands and along the Dutch mainland coast (van Dijk & Grootjans 1993; Ernst et al. 1996). When standing crop increases and organic matter starts to accumulate under conditions of no acidification, mowing and removal of biomass are good measures to keep nutrient availabilities low and to prolong the life-span of basiphilous pioneer vegetation (pers. observations in several dune slacks in the Dutch coastal area). Consolidation or reinforcement of the active buffering-mechanisms in dune slack environments are beneficial for basiphilous pioneer species. However, measures for this purpose, mostly in the field of water management, are sometimes difficult to specify and even more difficult to realize (Grootjans et al. 1996; Sival et al. 1997).

Acknowledgements. We are grateful to Jacob Hogendorf and Peter Grootjans for field assistance and sorting out the samples, to Nelly Eck and Willem van Hal for analysing the soil samples and to Dick Visser for preparing the figures. The Osmocote was kindly supplied by Sierra Chemical (De Meern, NL). Jelte van Andel and Eddy van der Maarel made valuable comments on an earlier draft.

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Received 16 July 1997;
Revision received 8 June 1998;
Accepted 23 September 1998.